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STUDIES IN THE CAPPARIDACEAE II.¹ THE MEXICAN SPECIES OF CLEOMELLA: TAXONOMY AND EVOLUTION

HUGH H. ILTIS

The Mexican species of *Cleomella*, a small North American genus of the Capparidaceae, are poorly known despite the fact that the genus was recently monographed by Payson (1922) and has received some attention since by West Coast floristic workers. During the preparation of a treatment of the Capparidaceae of Nevada (Iltis, 1955) and a phylogenetic study dealing with some North American Cleomoideae (Iltis, 1956), many specimens of *Cleomella* were examined. In the present study, a new species (*Cleomella perennis*) is described, the already-described taxa are more accurately delimited, some nomenclatorial problems are clarified, and certain aspects of the evolution of the taxa are discussed.

An examination of the specimens labelled *C. longipes* Torr. at the United States National Herbarium revealed that these could be separated easily into two groups on the basis of both morphological characters and geographic distribution. The specimens from the area including northern Mexico (Chihuahua), southwestern Texas, and southeastern Arizona (*C. longipes* Torr., *sensu stricto*) are all rather robust annuals with an erect stem or leader and with relatively large leaves, while those from Durango, Zacatecas, San Luis Potosí and Guanajuato in central Mexico (*C. perennis*) are all perennials with strongly thickened caudices, slender, decumbent or ascending branches, much smaller, narrower leaves, and fewer-seeded silicles. Despite these rather marked differences, the northern and southern populations have been classified under the same name for over one hundred years, largely because the shape of the fruit and length of the gynophore are nearly identical, two criteria usually of critical importance in other Cleomoideae. The only other Mexican species, the rare *Cleomella mexicana* Moc. & Sessé in DC., of the south-central Mexican plateau, is easily distinguished from its two northern relatives by its very short gynophore, small leaves, and prostrate branches. As was recognized by de Candolle (1824), it, too, is perennial, with a woody caudex and rootstock which is well illustrated in the "type-drawing" (cf. p. 182). This condition, occurring in two out of the three Mexican species of *Cleomella*, was completely overlooked by Payson (1922), who considered all species of the genus as annuals.

¹ The present study was made while the author was on the staff of the Department of Botany, University of Arkansas, Fayetteville, where he has had support from the Institute of Science and Technology, College of Arts and Sciences, and a grant-in-aid from the Society of Sigma Xi, to both of which he would like to express his thanks.

I. TAXONOMY

CLEOMELLA DC. Prodr. 1:237. 1824. (Type: *C. mexicana* Moc. & Sessé in DC.). *Isopara* Raf. Atl. Jour. 1:144. 1832. (Based on *C. mexicana* Moc. & Sessé in DC.). *Hyponema* Raf. Good Book 40. 1840. (*nom. nov.*). *Cleomella* DC. 1824). *Cleome* sect. *Cleomella* (DC). Baill. Hist. Plant. 3:149. 1872.

Erect to decumbent, unarmed, slender to robust, annual or perennial herbs, glabrous (except *C. obtusifolia*). Leaves 3-foliolate; leaflets entire, mucronulate, less than 4 cm. long, more or less thick, stipulate, the stipules minute, hyaline, filiform, usually less than 3 mm. long. Racemes terminal, usually bracteate, the bracts either 1-foliolate or the lower 3-foliolate, or flowers borne singly in the axils of caudine leaves. Sepals very small, free or basally connate, tardily deciduous. Corolla closed (convolute) in the bud; petals yellow, sessile or subsessile. Disk small, frequently expanded adaxially. Stamens 6, the anthers tightly coiled when dry. Fruit a small obdeltoid, rhomboidal, deltoid or ovoidal silicle, usually wider than long, often compressed contrary to the placenta, the valves usually conical. Silicles borne on short to elongate gynophores, the indurate, persistent styles usually setulose. Seeds 2–12 (–19) in each silicle, free-falling, the two claws formed by the invagination of the testa fused nearly their whole length, with only a trace of an internal sinus between them; testa usually smooth and often delicately marked (colliculate).

A genus with ten species, endemic to the western United States and Mexico; very closely related to *Cleome* sect. *Peritoma* (DC.) Baill., from which it differs principally in the smallness and shape of the fruit.

KEY TO THE MEXICAN SPECIES OF CLEOMELLA

- A. Leaflets of principal leaves 15–30 mm. long, 3–10 mm. wide; plants annual, from a usually slender taproot, with a branched or unbranched main stem (leader) usually simple at the base, the branches strongly ascending; Chihuahua to southwestern Texas and southeastern Arizona..... 1. *C. longipes*
- AA. Leaflets of principal leaves 5–14 mm. long, 1–5 mm. wide; plants perennial, much branched at the base from a greatly thickened, short woody root and caudex, the branches ascending to decumbent or procumbent.
 - B. Gynophore of fruit 11–16 mm. long; seeds 2.2–2.6 mm. long; branches ascending to decumbent, to 7 dm. long, the plants up to 5 dm. tall; Durango to San Luis Potosí and Guanajuato..... 2. *C. perennis*
 - BB. Gynophore of fruit 0.4–2.0 mm. long; seeds 1.9–2.0 mm. long; branches decumbent or prostrate, to 3 dm. long, the plants rarely over 1 dm. tall; Mexico, D. F. and northern Pueblo 3. *C. mexicana*
- 1. **CLEOMELLA LONGIPES** Torr. in Hook. Jour. Bot. & Kew Gard. Misc. 2:255. 1850; in Gray, Plantae Wrightianae 1:11. 1852 [Smithson. Contr. Knowledge 3 (Art. 5):11], *pro parte*, including the lectotype, Gregg 544!; excluding the Gregg San Luis Potosí specimen [herein cited under *C. perennis* Iltis].

Robust, glabrous, erect annual from an usually unbranched or little-branched taproot, 3–8 dm. tall, unbranched or more frequently with sev-

eral, strongly ascending branches, these usually scattered above the lower one-fourth of the erect main stem (leader), with only few branchlets, the main stem 2–6 mm. in diam.; petioles 7–30 mm. long, the petiolules 1–2 mm. long; leaflets oblanceolate to oblong-oblanceolate, acute to rounded or rarely emarginate, attenuate to the base from near the middle, 15–30 mm. long, 4–10 mm. wide, flat or conduplicate; racemes well defined, dense, greatly elongating in fruit, to 30 cm. long, bracteate or the upper portion ebracteate, the bracts 3-foliolate below, unifoliolate and reduced above; sepals connate at the base, triangular-lanceolate, acuminate to caudate-acuminate, 1.5–2.5 mm. long, tardily deciduous; petals oblong or lanceolate-oblong, obtuse to rounded, usually abruptly contracted into a short claw (5–)6–9 mm. long, 2–3 mm. wide; staminal filaments 8–12 mm. long; anthers 2.0–3.5 mm. long; ovary exserted on long gynophore; mature silicles obdeltoid to rhomboidal, 4–7 (–11) mm. long, 6–12 mm. wide, the style 1–2 mm. long; gynophore (6–)10–17(–21) mm. long, usually yellowish; pedicel (5–)7–15(–18) mm. long; seeds (4–)8–16 (–19) in each silicle, obovoidal, 1.9–2.4 mm. long, 1.4–2.0 mm. wide, 1.0–1.2 mm. thick, when mature dark brown, with the prominent lip of the shorter claw yellowish.

Chisos Mountains of southwestern Texas to the Chiricahua Mountains of southeastern Arizona, south to southern Chihuahua, Mexico, at elevations of 2500–5000 feet, in saline, alkaline soils or sands of semi-deserts, at edges of playas, old lake beds, thickets, ravines, and valleys, sometimes in *Tamarix-Prosopis* association, flowering and fruiting from late April to late September.

UNITED STATES: ARIZONA. County unknown: *D. T. McDougal*, s.n. (US).² Cochise County: west of the Chiricahua Mountains, *Wright* 857 (MO); 3 miles west of Willcox, *Darrow*, *Phillips & Pultz* 1045 (US). NEW MEXICO. Hidalgo County: Dog Spring, Dog Mountains, *Mearns* 2379 (US), *Hershey* s.n. (ILT, NMC). TEXAS. County unknown: Near J. Davis' ranch, West Texas, *Havard* 135 (US). Brewster County: Chisos Mountains area, in ravine of Rio Grande valley, *Sperry* 136 (US); near Chisos Mountains, *Young* 101 (MO); Rio Grande valley near Terlinguas, *Palmer* 34215 (MO); 3 miles southeast of Chilocal Mountain, *Marsh* s.n. (F). Hudspeth County: Rio Grande near Indian Hot Springs, *Waterfall* 4856 (MO). Presidio County: Penitas Ranch, 24 miles south of Marfa, *Hinckley* 1050 (F); near Chinati Mountains, *Hinckley* 824 (F). MEXICO. CHIHUAHUA. Near San Pablo, April 29, 1847, *Gregg* 544 (MO); Rio Palotat near Janos, *Schott* s.n. (F); Casas Grandes, *Goldman* 436 (US); Colonia Diaz, *Nelson* 6434 (US).

Torrey, in his original description of *C. longipes*, lists only two specimens, both collected by Dr. Gregg, one from Chihuahua and the other from San Luis Potosí. In the Missouri Botanical Garden Herbarium there are three Gregg collections, all of which can be considered isotypic, two of 544 labeled as from Chihuahua and clearly belonging to the northern taxon (*C. longipes sensu stricto*) and a third without any data except the

² The herbarium abbreviations used in the species citations, except for ILT, which refers to specimens in my own study collection, are those proposed by Lanjouw and Stafleu, Index Herbariorum, Regnum Vegetabile 2¹:106–117. 1952.

collection number (579). The latter is evidently the specimen from San Luis Potosí mentioned by Torrey, for it agrees in every respect with the other collections from that state, which belong to the southern entity mentioned in the introduction (*C. perennis*). Torrey thus established *C. longipes* on two collections belonging to two distinct though closely related taxa. His very generalized description offers no clue as to which of the two collections was primarily used by him in establishing *C. longipes*. Payson (1922), in his revision of *Cleomella*, likewise did not distinguish between the two taxa included in Torrey's *C. longipes*, undoubtedly because of the small number of specimens available to him for study. He did, however, choose the Chihuahuan *Gregg* collection as the lectotype, thus permanently associating the name *Cleomella longipes* with the plants from north-central Mexico and the adjoining United States. Kearney and Peebles (1942, p. 373) cite *Wright* 857, from the Chiricahua Mountains, as the type of *C. longipes*. This is an error, for the specimen was not cited by Torrey in the original description.

The specimens from the Chisos Mountains, the easternmost station of *C. longipes*, apparently represent a local race characterized by wider, emarginate leaflets, stronger connation of sepals, shorter anthers, and lower number (4–5) of seeds, which are larger than average.

2. *Cleomella perennis* sp. nov. Herbae glabrae vel minutule pilosae, perennes basi ramosae e caudice lignoso crasso; rami annui plus minusve suffruticosi, interiores erecti et ca. 15–50 cm. alti, exteriores decumbentes adscendentes, longitudine ad 70 cm.; folia densa, petiolis brevibus (2–10 mm.); foliola oblanceolata-cuneata 5–14 mm. longa, 1–4 mm. lata, apice rotundato vel emarginato; bractae racemi uni- vel tri-foliolatae, superne graduatim decrescentes; petala spatulata, 4.5–7.2 mm. longa, sepala triplo superantia; stamna et ovarium corollam duplo superantia; siliculae maturae obdeltoideae vel deltiodeae, 6–12 mm. latea; gynophorum gracillimum 11–16 mm. longum; semina subgloboso-reniformia, 2.2–2.6 mm. longa, 1.7–2.2 mm. lata, 3–7 per siliculam.

Holotypus. *C. G. Pringle*, Plantae Mexicanae 3089, in U. S. Nat. Herb. No. 1418485 ("Saline Plains, Salinas, San Luis Potosí, Mexico, June 30, 1890"). Isoty whole in Herb. BR, F, ILT, MO, MSC, SMU, et W.

Slender, more or less suffruticose and bushy, glabrous or minutely pubescent perennial herbs, much branched mainly from the apex of the greatly thickened, woody caudex (short and to 2 cm. in diam.) the clustered and branched annual stems 1–2(–3) mm. in diam., the inner erect and 15–50 cm. tall, the outer ascending to decumbent and up to 70 cm. long, densely leaved and frequently with many, very short branchlets; petioles 2–10 mm. long; petiolules 1 mm. long or less; leaflets narrowly oblanceolate-cuneate, rounded to emarginate, mucronulate, gradually attenuate to the base from near the apex, 5–12(–14) mm. long, 1–5 mm. wide, usually strongly conduplicate; racemes well-defined, dense, greatly elongating in fruit, up to 25 cm. long; lower bracts trifoliolate and like the foliage leaves, much reduced and either trifoliolate or unifoliolate

above; sepals joined at the base, broadly to narrowly triangular, acuminate to caudate-acuminate, 1.3–2.2 mm. long, tardily deciduous; petals oblong to lanceolate-oblong or oblanceolate, obtuse, gradually tapering to the base, 4.5–7.2 mm. long, 1.8–2.8 mm. wide; staminal filaments 10–14 mm. long; anthers 1.6–2.7 mm. long; ovary exserted on long gynophore; mature silicles obdeltoid, rhomboidal or deltoid, (3–)5–7 mm. long, 6–12 mm. wide; style 0.9–1.5 mm. long; gynophore 11–16 mm. long, usually dark purplish; pedicel 7–14 mm. long; seeds (3–)5–7 in each silicle, broadly obovoidal to subglobose, 2.2–2.6 mm. long, 1.7–2.2 mm. wide, 1.3–1.7 mm. thick, when mature brown to brownish-black, sometimes mottled, shiny, with the usually prominent lip of the shorter claw yellow-brown to whitish.

Mexico, from central Durango east to central San Luis Potosí and northern Guanajuato, at elevations near 6000 feet, in saline plains, ciénega bottomlands in grama grasslands (Gentry), steppes, ditches in grassy plains, and in sunny uncultivated fields; flowering and fruiting from late June into October (December).

MEXICO. DURANGO. City of Durango and vic., *E. Palmer* 1896–326 (F, ILT, MO, US); 40 miles north of Ciudad Durango, *Gentry* 8587 (US). ZACATECAS. 9 miles south of Villa de Cos, on road from Sierra Hermosa southwest to Zacatecas, *Johnston* 7437 (F, US), *Shreve* 8623 (US). SAN LUIS POTOSÍ. Salinas, *Pringle* 3089 (BR, F, ILT, MO, MSC, SMU, US type, W); Charcas, *Lundell* 5587 (US); San Francisco, *Gregg* 579 (MO, cited by Torrey as *C. longipes*). GUANAJUATO. Jaral, *Schuman* 311 (ILT, M, US) *Schnée* s. n. (ILT, P).

The Pringle collection was chosen as the type because of the widely distributed isotypes and the excellence of the material which includes not only flowers and nearly mature fruits, but also well developed caudices, so often left behind by most "hay-baling" collectors. Its bracts are 1-foliolate. Palmer's Durango collection, also widely distributed, supplements the type by its mostly 3-foliolate bracts and fully mature seeds and fruits. The two collections from Zacatecas cited above have unusually large caudices.

Cleomella perennis is intermediate between, and very closely related to, the preceding and following species geographically as well as morphologically. Thus the fruit and gynophore are nearly identical with those of *C. longipes*, the caudex and leaves with those of *C. mexicana*. In habit, size, erectness and most other attributes, *C. perennis* is exactly intermediate. Only the larger seeds and the lower seed number are out of line. As will be discussed presently, it is probable that *C. longipes* gave rise to *C. perennis*, which in turn is ancestral to *C. mexicana*.

3. *CLEOMELLA MEXICANA* Moc. & Sessé in DC. Prodr. 1:237. 1824; A. DC. Calq. Dess. Fl. Mex. Moc. & Sessé, t. 19. 1874. *Isopara mexicana* (Moc. & Sessé in DC.) Raf. Atl. Jour. 1:144. 1832. *Cleome mexicana* (Moc. & Sessé in DC.) D. Dietr. Syn. Pl. 2:1068. 1840, non *Cleome mexicana* Hemsl. Bio. Centr. Amer. Bot. 1:41. 1879.

Cleomella medicagineae Turcz. in Bull. Soc. Nat. Mosc. 27:313. 1854,
ex char. (Type: *Galeotti* 7216). *Physostemon medicagineum* (Turcz.)
Briqu. in Ann. Conserv. & Jard. Bot. Genève, 17:390. 1914.

Slender, herbaceous or somewhat suffruticose perennials from a stout taproot and caudex, 1–2 dm. tall, profusely branched, particularly from the base, the clustered branches strongly decumbent, 10–25 cm. long, 1–2 mm. in diameter; petiole 5–13(–19) mm. long; petiolules 1 mm. long or less; leaflets thick, cuneate-obovate, truncate to emarginate, gradually attenuate to the base from above the middle, 3–11 mm. long, 2–5 mm. wide, strongly conduplicate; racemes lax and ill-defined, not greatly elongating in fruit, the flowers borne near the tip of the branches in the axils of full-sized or slightly reduced 3-foliolate leaves; sepals barely joined at the base, lanceolate, acuminate, 1.3–1.7 mm. long, deciduous; petals broadly oblanceolate, rounded, gradually attenuate to a broad base, 3.5–4.2 mm. long, 1.5–1.9 mm. wide; stamens included, the filaments 2–3 mm. long; anthers 1.2 mm. long; ovary included; mature silicles obdeltoid to rhomboidal, 3–5 mm. long, 6–9 mm. wide; style 0.3–0.5 mm. long; gynophore 0.4–2.0 mm. long, purplish; pedicel 8–11 mm. long; seeds 6–8 (–10?) in each silicle, obovoidal, 1.9–2.0 mm. long, 1.5–1.6 mm. wide, 1.1–1.2 mm. thick, brown, the lip of shorter claw not conspicuous.

In saline plains, in the vicinity of Mexico City and Tepeyahualco, Pueblo, at elevations of 7000–7700 feet, flowering and fruiting from May to late September (December).

MEXICO. Sessé, Mociño, Castillo & Maldonado 3356 (MA); between Vera Cruz and Mexico City, Halstead s.n. (MO). MEXICO, D. F. Mexico City, Rutten & Rutten-Pekelharing 438 (ILT, U). PUEBLO. Prope Tepeyahualco, Schiede & Deppe s.n. (M.).

Cleomella mexicana, the type of the genus, is fairly well illustrated in Sessé and Mociño's unpublished "Icones Florae Mexicanae," which were copied by the ladies of Geneva for the elder de Candolle before the plates had to be returned to Madrid (cf. Standley, 1920, p. 16). Tracings of these copies (A. de Candolle, 1874) are in the library of the Missouri Botanical Garden, *Cleomella mexicana* being plate 19. A Macbride photograph (No. 30454) of the original water color copy now at Geneva is in the herbarium of the Chicago Natural History Museum. Since the only thing de Candolle had at hand when he described the species was this Sessé and Mociño plate, it must be taken in lieu of the type. However, in the Instituto Botánico "Antonio José Cavanilles," Madrid, there is a sheet with abundant specimens of *Cleomella mexicana* collected by Sessé, Mociño et al.

Judging from the description, *Cleomella medicaginea* Turcz. is clearly the same as *C. mexicana*. It is based on a collection of Galeotti's from "planitia salsa prope urbem Mexico." *Cleomella medicaginea* was later transferred by Briquet (1914, p. 390) to *Physostemon* (as *P. medicagineum*), a quite unrelated group, because he thought Turczaninow's species to be identical with Hemsley's *Cleome mexicana* (1879), and wanted

to conform to the rules of priority, for Hemsley's *Cleome mexicana* indeed does belong to *Physostemon*, a *Cleome* segregate with unifoliolate leaves and apophysate stamens.³

The exact localities where *Cleomella mexicana* has been collected have never been cited with the collections. It is almost certain though that the "salt-lake" Lago de Texcoco (alt. 2236 m.), east of Mexico City, which was drained in 1920, was the location for the specimens labelled as coming from Mexico City, and that the series of large salt-flats south and southwest of Tepeyahualco are likewise the origin of the collection labelled as coming from that town. As a matter of fact, these are the only saline lakes reported on the *Hoja Puebla* (lat. 19°N., long. 97° 30'W.) topographic map (1:500,000; 1944) of the *Dirección de Geografía, Meteorología e Hidrología* of Mexico.

II. PHYLOGENY

Evolution in the subfamily Cleomoideae seems to have progressed in many instances from types inhabiting mesic habitats to those growing in deserts or semi-deserts. Certain recurrent evolutionary trends represent not only evolution from the more primitive to the specialized morphological type but, more specifically, the evolution of structures more closely in harmony with arid and/or alkaline habitat requirements. Similar trends occur in the New World not only in *Cleomella* but also in quite unrelated groups of species (e.g., the unifoliolate species of *Cleome*, including *Physostemon*), as well as in various groups of the Old World.

The following list of evolutionary tendencies in the Cleomoideae applies mainly to the genus *Cleomella*, especially the Mexican species, but would hold true for all its close relatives (viz. *Cleome* sect. *Peritoma*, *Wislizenia*, *Oxystylis*) and, with a little modification, for most other xerophytic Cleomoideae as well. Some of these conclusions are at variance with present day phylogenetic points of view. A full explanation of the reasons for considering characters primitive or specialized in the Western North American Cleomoideae (exclusive of *Polanisia*) are given in a forthcoming study (Iltis, 1956) dealing with the morphology and phylogeny of the species of *Cleome* Section *Peritoma*, *Cleomella*, *Wislizenia*, and *Oxystylis*. In Table 1 characters that occur in *Cleomella longipes* are indicated by (1), those that occur in *C. perennis* by (2) and in *C. mexicana* by (3).

³ Hemsley's *Cleome mexicana* of 1879 (in *Biologia Centrali-Americanica, Botany* 1:41) was invalid because preoccupied by *Cleome mexicana* (Moc. & Sessé in DC.) D. Dietr. 1840. (= *Cleomella mexicana*). To correct this, Bullock (in *Kew Bull. Misc. Inf.* 1936:388) renamed Hemsley's species *Cleomella hemsleyana* Bullock, thus assigning it to the wrong genus. To place this taxon among its relatives, Foster (in *Contr. Gray Herb.* 155:58. 1945) transferred it to *Physostemon* [as *P. hemsleyanum* (Bullock) Foster]. In my opinion, it is not possible to segregate *Physostemon* from the unifoliolate New World species of *Cleome*. It therefore becomes necessary to return the invalid *Cleome mexicana* Hemsley to *Cleome* as *C. hemsleyana* (Bullock) Iltis, comb. nov. (Type: *Galeotti* 3194, K!).

TABLE 1. COMPARISON OF PRIMITIVE AND SPECIALIZED CHARACTERS IN MEXICAN SPECIES OF CLEOMELLA AND RELATED TAXA

A. Primitive	B. Specialized
1. Annual with little branched taproot. (1)	Perennial with roots from a woody caudex or rootstock. (2-3)
2. Plants large (1-6 m.).	Plants small (1-100 cm.). (1-3)
3. Stems simple at the base with unbranched main leader. (1)	Stems much branched from the base without a main leader. (2-3)
4. Stems erect or strongly ascending. (1-2)	Stems decumbent to prostrate. (2-3)
5. Leaves estipulate.	Leaves with minute "stipular" structures. (1-3)
6. Leaves large, 3- to 13-foliate. (1)	Leaves small, 3- or 1-foliate. (1-3)
7. Leaves long-petioled. (1, 3)	Leaves short-petioled to sessile. (2-3)
8. Leaflets at apex caudate-acuminate to acute, at base long-attenuate. (1)	Leaflets obtuse to emarginate at apex, cuneate to rounded at base. (1-3)
9. Leaflets lanceolate-elliptic. (1)	Leaflets oval to obovate. (1-3)
10. Leaflets thin, with many raised lateral nerves.	Leaflets thick, with only the midrib and few immersed, nearly obsolete lateral nerves. (1-3)
11. Leaflets more or less flat. (1)	Leaflets strongly conduplicate. (2-3)
12. Flower and fruit production after much vegetative growth. (1-2)	Flower and fruit production after little vegetative growth. (2-3)
13. Racemes bracteate. (1-3)	Racemes ebracteate. (rarely in 1)
14. Flowers in well defined terminal racemes. (1-2)	Flowers in the axils of cauline leaves (associated with 4B). (3)
15. Bracts 1-foliate. (1-2)	Bracts 3-foliate or like cauline leaves. (2-3)
16. Post-floral elongation of raceme axis very pronounced.	Post-floral elongation of raceme axis small.
17. Nectary small, smooth.	Nectary relatively large, variously sculptured, etc. (1-3)
18. Petals large. (1-2)	Petals small. (3)
19. Stamens and ovary long-exserted. (1-2)	Stamens and ovary included or nearly so. (3)
20. Stigma large, capitate, sessile.	Stigma minute, truncate or pointed, on slender style. (1-3)
21. Fruits terete, linear-cylindric, large and long (5-25 cm.), many-seeded.	Fruits compressed, various, small and short (1-3 cm. or less), few-seeded. (1-3)
22. Fruits with deciduous valves, and free-falling seeds. (1-3)	Fruits with persistent valves separating only at apex, or with valves that permanently enclose seeds.
23. Gynophore long. (1-2)	Gynophore short. (3)
24. Seeds with large internal sinus.	Seeds with obsolete internal sinus. (1-3)

The somewhat unusual conclusion that the perennial woody caudex of the Cleomoideae is a derived or specialized structure is based primarily on the fact that in the Mexican species of *Cleomella*, where all traits except for minor exceptions (see below) follow interrupted clines from north to south, all of many characters (except for the problematic one of duration) are in the primitive state in the northern *C. longipes*, in the special-

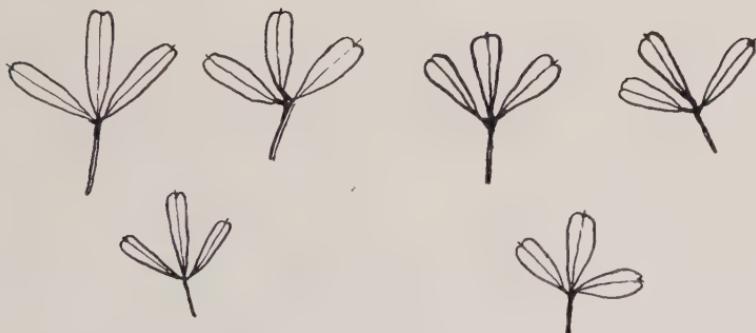
C. LONGIPES**C. PERENNIS****C. MEXICANA**

FIG. 1. Principal cauline leaves of the Mexican species of *Cleomella*. Natural size.

ized state in the southern *C. mexicana*, while the geographically intermediate *C. perennis* is morphologically intermediate also (cf. figs. 1 and 2). Secondly, the reputed ancestors of *Cleomella* (see below) are all annuals. Thirdly, parallel situations exist in *Wislizenia* (Greene, 1906) and in

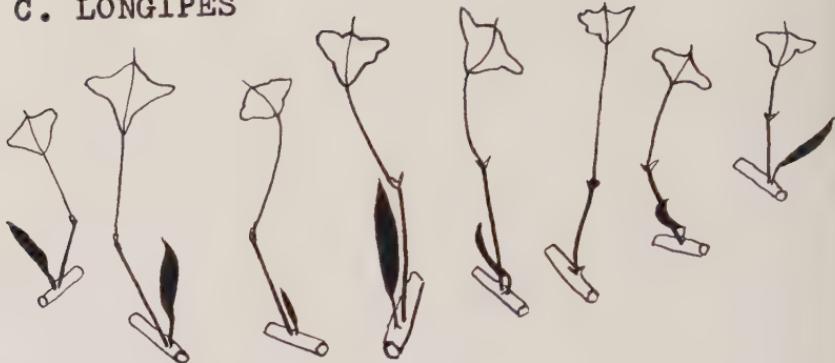
C. LONGIPES**C. PERENNIS****C. MEXICANA**

FIG. 2. Mature silicles and bracts of the Mexican species of *Cleomella*. Natural size. Each fruit from a different collection, except the lower left two, where the first shows the usual dimerous silicle, and the second the rare, abnormal trimorous fruit.

several groups quite unrelated to *Cleomella* which leave little doubt that in certain arid climes evolution may proceed from the annual to the perennial habit. For example, in the phyletic sequence of the unifoliolate Cleomoideae (and relatives) of the New World, the primitive taxa (*Cleome tenuis*, *C. stenophylla*) are annuals, while the more specialized forms had evolved the perennial habit in at least two separate lines: 1) in the West Indian semi-desert species (*C. wrightii*, *C. macrorhiza*, etc.) and 2) in the highly specialized taxa commonly classified under the genus *Physostemon*, which are native to the arid "Caatinga" of northeast Brazil and to the southern Mexican grasslands.

Therefore, the perennial woody rootstock of these plants which, according to Bessey (1915) and other workers, would indicate a primitive structure, must be thought of rather as a derived condition which had developed in the arid, alkaline inter-montane plateau region of central and southern Mexico, and in climatically similar regions, as an adaptation to that particular habitat type, a development which occurred in various groups at various times through convergent evolution.

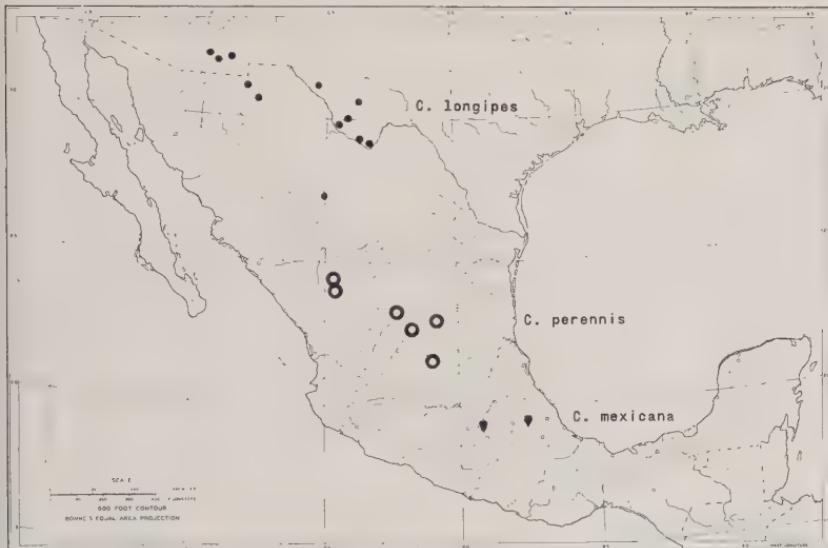


FIG. 3. Distribution of the Mexican species of *Cleomella*. (Base map Goode's copyrighted map 112 with permission of the University of Chicago.)

We can detect only two minor exceptions to the uniformly north-south sequences of nearly all morphological modifications: 1) in seed size, that of *C. perennis* being greater on the average than that of either of the two other species, and 2) in petiole length, the petioles of *C. perennis* being often shorter than those of either *C. longipes* or *C. mexicana*.

From this evidence, it seems reasonable to assume that in Mexico *Cleomella* migrated from north to south (fig. 3). To emphasize this, it should be pointed out that *Cleomella* as a genus is clearly derived from *Cleome* sect. *Peritoma* (DC.) Baill., of which the annual, erect, 5-foliate *Cleome lutea* of the western United States is probably most like the ancestor of *Cleomella*. *Cleomella angustifolia* of eastern Texas and Oklahoma, a tall, erect, 3-foliate annual, is very similar to *Cleome lutea*, particularly vegetatively. It is also very similar to *Cleomella longipes*, allopatric to the southwest, but has more acute, larger leaflets and larger, rugose seeds. These two appear to be the most primitive of all the 10 species of *Cleomella*.

The allopatric distribution of the Mexican taxa (fig. 3) also supports the belief that these three species of *Cleomella* are part of a single phylad

that originated in the Arizona-Texas region and migrated southward from there. This appears to me to be of considerable interest since the species of *Cleomella* are a typical part of the southwestern desert flora, the members of which are reputed to have migrated *north* from the Mexican plateau (Munz, 1935). While this has undoubtedly occurred in the case of the ancestors of the more primitive *Cleome* sect. *Peritoma*, the northward migration (at least here) was followed at a later and perhaps rather recent date by a southward migration of some of its more specialized descendants, namely the Mexican species of *Cleomella*.

Two additional north-south trends are found in the Mexican species of *Cleomella*. One, the tendency for a southward decrease in distributional area is evidenced here by *C. mexicana*, the southernmost of the species of *Cleomella*, as compared with the more northern species (fig. 3). It occurs in the only two available saline areas in the region around Mexico City. Because of this narrow ecological restriction, it might be considered homogenic (Stebbins, 1942). The second north-south trend is evidenced by the fact that the species of *Cleomella* occur at progressively higher altitudes towards the south: the northern *C. longipes* occurring at elevations of 2500–5000 feet, the central *C. perennis* at about 6000 feet, and the southern *C. mexicana* at 7000–7700 feet. This corresponds to the fact that given vegetational zones occur at higher elevations in lower latitudes.

III. SUMMARY

A new perennial species of *Cleomella* (*C. perennis*) is described from north-central Mexico. It is closely related to and intermediate between *C. longipes* to its north, an annual with larger leaves, and *C. mexicana* to its south, a perennial with low decumbent branches and smaller flowers. A preliminary list comparing primitive versus specialized characters in the Cleomoideae is presented, and the view is proposed that the perennial habit may, in some cases, be the specialized rather than the primitive condition. All data support the contention that *C. longipes* is most primitive and has given rise to *C. perennis* and *C. mexicana*. These species comprise a phylad which probably had a northern origin and a southward migration. Since the group ancestral to *Cleomella* (*Cleome* sect. *Peritoma*) originated from tropical stock that moved north to the region of the southwestern United States, the Mexican branch of *Cleomella* thus returned to Mexico on the route of its ancestors, but probably in drier habitats and at higher elevations. The southwestern desert flora which generally is considered to have originated from the flora of the semi-arid Mexican plateau, thus seems to have returned the favors to the latter by the contribution of some of its specialized, more recent derivatives.

Department of Botany,
University of Wisconsin, Madison

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TWO FUNGI ASSOCIATED WITH A MICROCYCLIC RUST,
COLEOSPORIUM CROWELLII CUMMINS, ON NEEDLES
OF *PINUS EDULIS* ENGELM. IN ARIZONA¹

PAUL D. KEENER²

The microcyclic rust, *Coleosporium crowellii* Cummins (Cummins, 1938) is unique among species of the genus because of the occurrence of the telial stage on species of *Pinus*. This species of *Coleosporium* is also regarded as autoecious. Other species of *Coleosporium* are macrocyclic with needles of certain pines serving as sites for the pycnia and aecia rather than the telia. In addition, species of *Coleosporium* are generally heteroecious.

Material of *C. crowellii* on *Pinus edulis* Engelm. was collected one mile east of Yaki Point, on the north side of State Highway 64 along the South Rim of the Grand Canyon, Grand Canyon National Park, Coconino County, Arizona, on October 6, 1953. The telial sori were of an unnatural dull yellow-brown, rather than the usual yellow-orange. The sori of the rust fungus were found to be invaded by two non-uredineous fungi, *Darluca filum* (Biv.) Castagne and *Cladosporium aecidiicola* Thüm. Both of the fungi were in their conidial phases. No previous reports of these two hyperparasites on this rust have been found.

Materials for microscopic examination were prepared in the following manner: small portions of pine needle tissue containing rust sori invaded

¹ Arizona Agricultural Experiment Station Technical Paper No. 364.

² Assistant Plant Pathologist, University of Arizona Agricultural Experiment Station, Tucson.

by the hyperparasites were placed momentarily in 95 per cent ethyl alcohol, then in lukewarm water for several minutes until softening occurred. Free-hand sections were then prepared. The sections were mounted in 0.25 per cent Orseillin BB in 3 per cent acetic acid and modified Sartory's solution. The Orseillin BB in acetic acid was added to the Sartory's solution (phenol, 10 cc.; lactic acid, 20 cc.; glycerine, 40 cc.; distilled water, 20 cc.) in the proportion of 1 part of the former to 9 parts of the latter. The technique is essentially the same as described by Alcorn and Yeager (1937) with slight modifications including adaptation to free-hand sections.

DARLUCA FILUM (Biv.) Castagne

Species of *Darluca* and especially *D. filum* have been reported as associated with numerous rust fungi (*Uredinales*) in many parts of the world. Most of the reports indicate that *D. filum* is more often found in uredinal and telial sori than in aecia. Also, there are more records of the association of this hyperparasite with macro- than with microcyclic rusts. The significant literature concerning the various genera of rusts reportedly susceptible to attack by *D. filum* in various parts of the world has been reviewed (Keener, 1934). In addition, previous investigations involving cross-inoculations with several isolations of *D. filum* from numerous rusts showed that many species of rusts are susceptible to attack by one or more forms of the hyperparasite (Keener, 1934; 1952). Isolations of *D. filum* from infected rusts in the field, cultured on "Difco" Lima Bean agar, were used as sources of inocula in the previous studies (Keener, 1933; 1934). The studies confirmed the fact that both macro- and microcyclic rusts are susceptible to attack by *D. filum*, if suitable environmental conditions prevail. Although not previously emphasized (Keener, 1934) it was found that no great morphological differences existed among the various isolations of *D. filum* from field-infected materials, and the same isolates after inoculations on rusts other than those from which they originated. The same was true of isolations of the hyperparasite from field-infected materials when inoculated in the greenhouse onto rusts similar to those from which they had been isolated.

The fungus found inhabiting telial sori of *Coleosporium crowellii* at Grand Canyon agrees in most morphological respects with the isolations of *D. filum* from various rusts studied previously (Keener, 1934). Some interesting differences were noted. In most cases previously recorded, pycnidia of the hyperparasite have been described as being superficial with respect to the area occupied by the rust sorus. In the Grand Canyon material of *D. filum* on *C. crowellii* this was not always true. Many of the pycnidia of *D. filum* were found at the bases of the telial columns of the rust, in close association with the basal teliospores (fig. 1). Since the basal teliospores themselves are actually embedded in the pine needle mesophyll, the pycnidia of *D. filum* are frequently invisible in the field even with the aid of a hand lens. Only at certain stages were pycnidia of the hyperparasite observed in the telial columns at a level with the needle

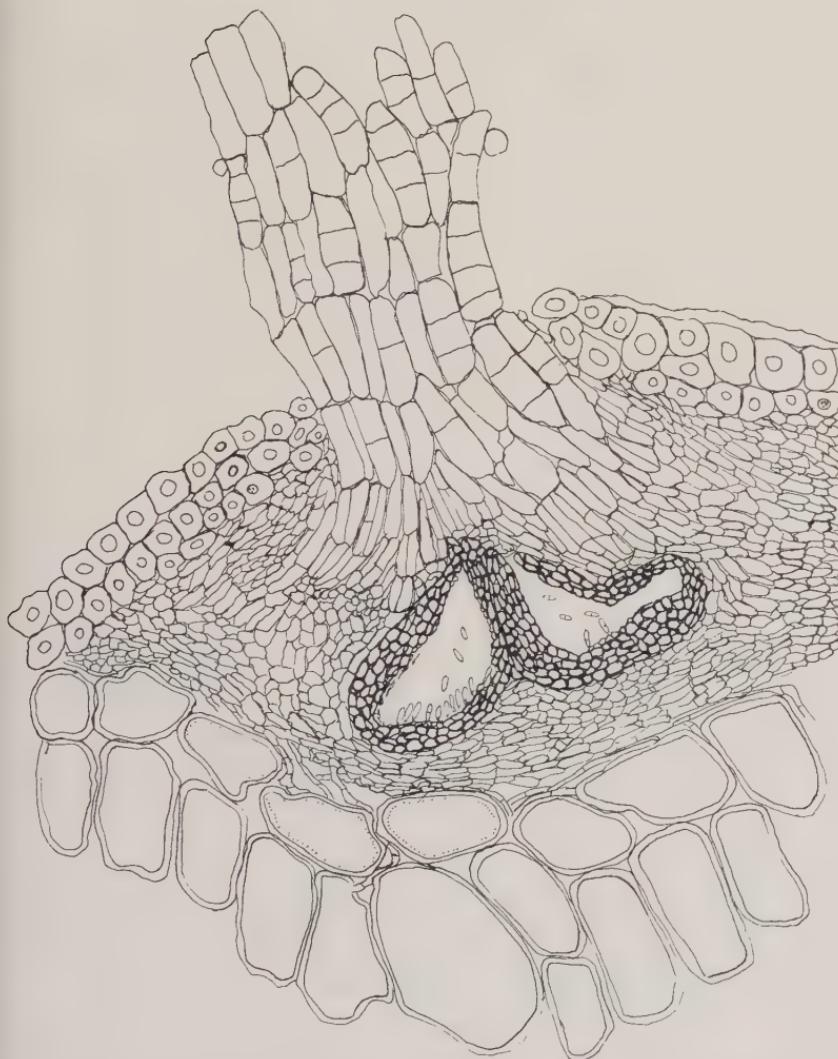


FIG. 1. Schematic representation showing two pycnidia of *Darluca filum* associated with basal teliospores in the telial column of *Coleosporium crowellii*. Magnification approximately $\times 270$.

epidermis or above. The invisibility of the pycnidia prevails until after the collapse of the telial column, at which time they may be observed to be superficial with respect to the rust sorus and the pine needle tissues. The invisibility of the pycnidia for considerable periods of time may account in part for the absence of any previous reports of *D. filum* associated with *C. crowellii*.

A peculiar feature of the invasion of telial sori of *C. crowellii* by *D. filum* is the manner in which the long, twisted, dark-brown, fragile spore threads of the hyperparasite reach the needle surface. These threads issue

from the region between the bases of the telial columns and the ruptured pine needle epidermis (fig. 2, B). The threads contain the typical 2-3-celled macroconidia of *D. filum* (fig. 3, A). Some of the fragility may be

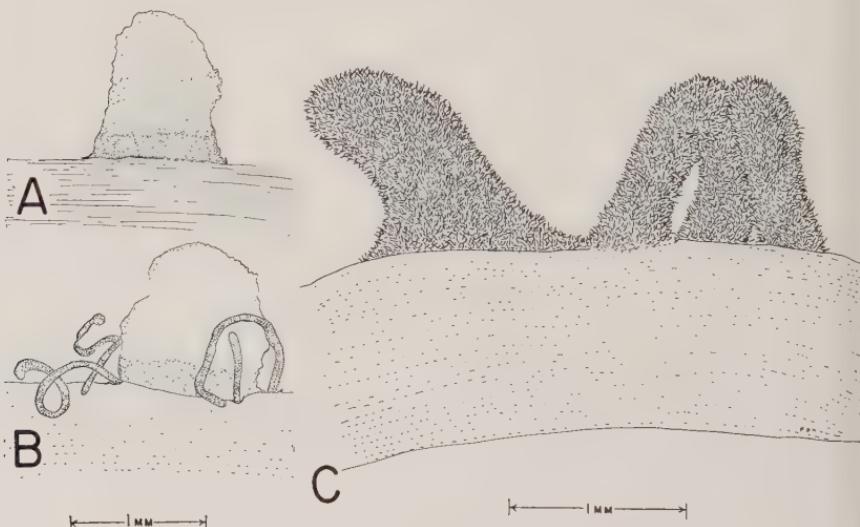


FIG. 2. Schematic drawings of telial columns of *Coleosporium crowellii* with associated fungi on needles of *Pinus edulis*. A. Telial sorus free of any invasion by hyperparasitic fungi. B. Spore threads of the hyperparasite, *Darluca filum*, issuing from between the pine needle epidermis and the base of the rust telial column. C. Conidiophores and other fungus structures of *Cladosporium aecidiicola* completely overrunning telia of the rust.

due to the prevailing dry atmosphere in Arizona. In spite of the desiccation of the spore threads, macroconidia germinated readily in sterile distilled water on glass slides in from 4-6 hours at room temperatures. Often the spore threads which are best observed with a dissecting microscope are the only visible evidence of rust sorus invasion. Non-invaded sori show no thread-like strands (fig. 2, A).

CLADOSPORIUM AECIDIICOLA Thüm.

Parasitism of rust fungi by species of *Cladosporium* has been reported in the past chiefly from the continent of Europe and the region of the Mediterranean. Some of the pertinent literature has already been reviewed (Keener, 1954). Of interest are two previous reports of this hyperparasite of rusts from the western United States (Keener, 1954; Smith, 1905).

In the Grand Canyon material of *Coleosporium crowellii* invaded by *Cladosporium aecidiicola* no preference by the hyperparasite for a particular region of the rust telial column was noted. The brown, septate hyphae and 1-2-celled yellow-brown conidia of *C. aecidiicola* (fig. 3, B), appeared to inhabit all parts of the telial sorus, frequently overrunning the entire column (figs. 2, C; 4). The telial columns inhabited by the

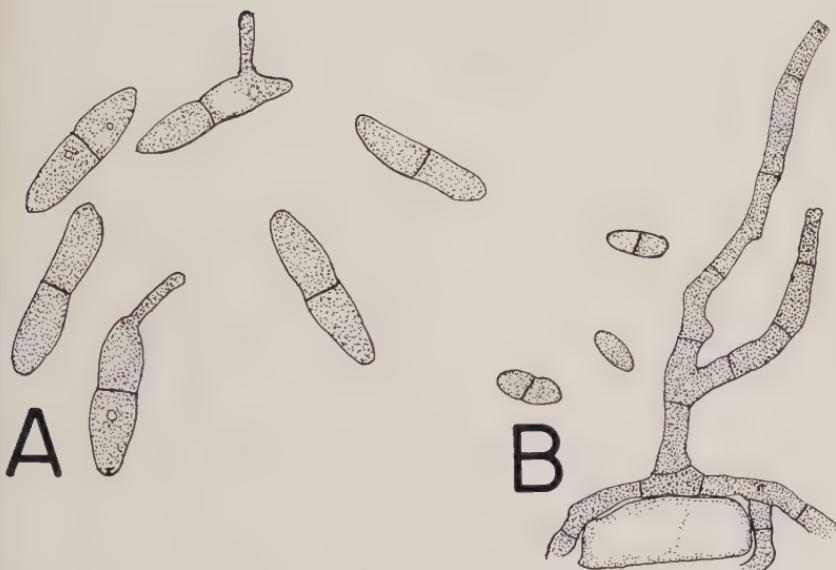


FIG. 3. Fungus structures of two hyperparasites associated with telial sori of the microcyclic rust, *Coleosporium crowellii* on *Pinus edulis*. A. Macroconidia, two of which show germ tubes, of *Darluca filum*. B. Conidiophores and conidia of *Cladosporium aecidiicola*. Magnification approximately $\times 300$.

hyperparasite were dark-brown to black rather than the dull yellow-brown color of sori inhabited by *D. filum*. Due to their dark color, telial sori of *Coleosporium crowellii* inhabited by *Cladosporium aecidiicola* are easily recognized in the field, their pigmentation contrasting strikingly with the yellow-orange color of non-invaded ones. Sori invaded by *C. aecidiicola* appear to collapse sooner and more completely than do those attacked by *D. filum*. This is probably due to the complete invasion of the entire telial column of the rust by *C. aecidiicola*.

The morphological features of the fungus referred to as *C. aecidiicola*

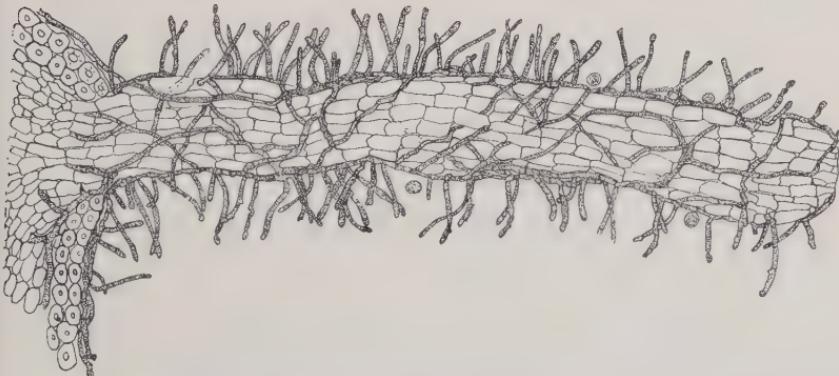


FIG. 4. Diagrammatic drawing showing a single telial column of the microcyclic rust, *Coleosporium crowellii* on *Pinus edulis*, completely invaded and overrun by the vegetative hyphae of the hyperparasite, *Cladosporium aecidiicola*. Magnification $\times 38$.

agree with those described for this species by other authors as well as with those of a similar fungus found inhabiting aecial sori of *Puccinia conspicua* (Arth.) Mains on *Helenium hoopesii* A. Gray in southern Arizona (Keener, 1954).

In October 1954, over forty specimens of *Pinus edulis* with needles on the lower branches attacked by *Coleosporium crowellii* were observed within the boundaries of Grand Canyon National Park, in the vicinity of Yaki and Moran Points. In spite of the below average rainfall during the preceding months, *Cladosporium aecidiicola* was widespread in many of the telial sori of the rust. This hyperparasite appeared to be more generally distributed in sori of *Coleosporium crowellii* than was *D. filum*. In 1954, *D. filum* was virtually absent in the Grand Canyon area on *C. crowellii*. Recently material of *Cladosporium aecidiicola* has been noted in aecial sori of *Cronartium quercuum* (Berk.) Miyabe on cones of *Pinus cembroides* Zucc. The hyperparasite has been isolated into pure culture from this material.

One specimen of *Pinus edulis* was found at Grand Canyon which had sori of *Coleosporium crowellii* invaded by *Cladosporium aecidiicola* and on the same or on different needles, fruiting bodies (hysterothecia) of *Elytroderma deformans* (Weir) Darker. The latter fungus is an Ascomycete and causes a needle-cast of conifers.

The assistance in securing permission to collect the necessary materials as well as the continued interest in the study proffered by Mr. Louis Schellbach, Park Naturalist for Grand Canyon National Park, is hereby gratefully acknowledged.

SUMMARY

1. Association of the hyperparasites, *Darluca filum* (Biv.) Castagne and *Cladosporium aecidiicola* Thüm. with telial sori of the microcyclic rust, *Coleosporium crowellii* Cummins on *Pinus edulis* Engelm., is reported for the first time.
2. Morphological similarities and differences between these associations and similar though not identical ones recorded previously are discussed.
3. The investigation is based on materials collected in the vicinity of Yaki and Moran Points, South Rim of the Grand Canyon, Grand Canyon National Park, Coconino County, Arizona.

Department of Plant Pathology,
College of Agriculture, University of Arizona, Tucson

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A NATURAL HYBRID, \times ADIANTUM TRACYI C. C. HALL¹

WARREN H. WAGNER, JR.

A plant intermediate between the two common maidenhair ferns of California, *Adiantum jordanii* K. Müll. and *A. pedatum* L., was first discovered over a half-century ago, but except for several brief references in British gardeners' publications (Stansfield, 1927; Macself, 1947; Logan, 1948), notes on it have never been published. The intermediate plant has now become established in horticulture both in California and in England, and is notable for its vigorous growth. Although the spores of this fern appear to be inviable, the rhizomes are capable of bearing numerous lateral shoots, enabling single plants to form large patches in gardens and to be readily propagated.

The fact that the plant described here is evidently intermediate between *A. jordanii* and *A. pedatum* in its obvious features is a strong point in favor of interpreting it as a hybrid between them. This conclusion is also supported by the following facts: the intermediate plant is rare and sporadic in distribution as compared with the much more abundant and widespread parents, and it has been found wild in only three counties of California; the supposed parents were present in the immediate vicinity of the putative hybrid; the sporangia of the intermediate are abortive and its spores are of irregular sizes and shapes. With such evidence indicative of hybrid origin I believe that it would be erroneous to name and describe this fern as a normal taxonomic species.

At the present time I know of only ten places where this plant is in cultivation but there are probably many more. In view of its luxuriant growth and graceful appearance it is likely to become widely distributed in horticulture. For this reason the information that has been gathered on the history of its discovery and spread in horticulture should be useful.

The intermediate fern was first found in September, 1895, by the late Joseph Prince Tracy, a well-known botanist of Eureka, California, whose

¹ Study made during the tenure of a Summer Faculty Research Fellowship of the Horace H. Rackham School, University of Michigan.

collection was recently bequeathed to the Herbarium of the University of California (biography, Bacigalupi, 1954). The fern—a single plant—was growing in redwoods along the Eel River, near the town of Pepperwood. Dr. Walter C. Blasdale has written (letter, August 27, 1953) as follows: "Only about three years ago I happened to meet Mr. Tracy and talked with him about it. He assured me that he found a small patch of it not far from plants of *A. pedatum* and *A. emarginatum* [syn. *A. jordanii*] and had never found other specimens of it anywhere else." The specimen which was taken by Mr. Tracy was grown in his garden for many years and gave rise to new rhizomes. One of these he presented to the late Mrs. Carlotta C. Hall, who considered the plant a hybrid and had long planned to name it in honor of Mr. Tracy. She was particularly interested in the variability of the branching shown by the leaf blades. The descendants of Mrs. Hall's plant produced a luxuriant clone in her garden at Berkeley, and she contributed living specimens to the Strybing Arboretum in Golden Gate Park, San Francisco, as well as to friends, including Dr. Blasdale, who found it a remarkably fine fern for out-of-door cultivation.

There is evidence that this apparently hybrid fern has arisen independently in the wild on four other occasions. For information regarding several of these I am indebted to Mr. Hugh B. Logan. He possesses living specimens from four different original localities growing in his garden at Inverness, Marin County, California, and a number of the following notes are taken from his letters about them.

Mrs. Mabel Bishop, the daughter of Mrs. Frances Mason, around 1910–1915, discovered plants morphologically like Mr. Tracy's growing near Guerneville on the Russian River in Sonoma County. Mrs. Mason subsequently presented living material of one of these to Mr. Carl Purdy of Ukiah, California, who then included this fern in the many native plants he sold. It was Mr. Purdy who introduced the plant in England; he sent it originally to Mr. Amos Perry of Enfield, Middlesex, England, who distributed it. The fern proved to be hardy there and was called "*Adiantum flabellulatum*," but was considered even then to have originated by hybridization—"possibly a cross between *A. pedatum* and *A. capillus-veneris*, and consequently a sort of British-American hybrid" (Stansfield, 1927). The fern was described as being similar in habit to *A. pedatum*, but the rhizome is less wide-creeping and the plant is thoroughly evergreen. According to Mr. Logan, who has sent specimens to relatives in Wales, it can withstand the English winter.

This fern was also, according to further information supplied by Mr. Logan, discovered in Bear Valley, Marin County, California, where Mrs. Slate Weston removed a plant and transferred it to her garden. From her Mr. George Syme obtained living specimens, and he subsequently returned to the Bear Valley area himself to search for the plant *in situ* but had no success in finding it. Mr. Syme cultivated the plant at Petaluma, Sonoma County, and sent a number of fine fronds to the Smithsonian Institution in 1919. Plants from the Bear Valley stock were included in Carl



FIG. 1. *× Adiantum tracyi* C. C. Hall. A perfect frond of the plant found by Mr. J. Neeman near Garberville, Humboldt County, California.

Purdy's collection, and some of these were sent, along with the Russian River plants, to Mr. Perry in England. Mr. Logan has also written me that he possesses additional plants which came from the south fork of the Gualala River, Sonoma County, and which were given by an Indian girl to Mrs. Celestine Levens of San Rafael.

In 1948, Mr. James Neeman of Garberville, California, sent a small but unmistakeable frond of the hybrid to the National Herbarium (illustrated in fig. 1) and he has recently (letter, April 25, 1954) written of the circumstances of finding this specimen as follows: "Regarding the *Adiantum* hybrid I discovered in Humboldt County, it grew about a mile and a half north of the town of Garberville. . . . The area is cut by small streams and high hills. In the deep, cool, shady gulches one finds redwoods, pepperwoods, and on the drier slopes, fir, madrone, and oak. I

was following the stream upwards in a deep glen where woodwardias, *Polystichum munitum*, and an occasional *P. californicum* grew, the gold-back [*Pityrogramma triangularis*] with *Adiantum jordanii* covering mossy slopes on the drier slopes and facing north on a sandstone cliff, I saw five-fingers [*Adiantum pedatum*] near by. Among them, I could discern the triangular forms of the hybrids, all told, nine of them, mostly small plants."

Mr. Neeman has written also that "peculiarly, the fern is almost evergreen, unlike its parents." *Adiantum jordanii*, on the contrary, holds its foliage for only a few months and then dries down completely; it is usually an inhabitant of dry situations, and sends up its fronds in the spring before *A. pedatum*. In this respect, the intermediate plant resembles *A. jordanii* more and the "hybrids start in the spring before *A. pedatum* shows any growth." (Logan, letter, April 10, 1954). The hybrid fern also seems to be quite resistant to injury, and Mr. Neeman informs me that three plants, each growing in a three-gallon can, were scorched to the ground when his house burned down, but since then they have begun to come up again and are now growing well once more.

I wish to thank the persons mentioned for the information given above concerning this plant's history. I am indebted also to Mr. Conrad V. Morton of the U.S. National Herbarium and Dr. Herbert L. Mason and Miss Annetta Carter of the University of California Herbarium, for lending dried specimens. To facilitate this study, Mrs. R. S. Nicolls, daughter of Mrs. Hall, kindly collected from her mother's Berkeley garden a number of dried leaves and a living rhizome.

Adiantum tracyi C. C. Hall, hybr. nov. *Adiantum A. jordanio A. pedatoque intermedium*, *laminæ foliorum late deltoideæ*, *e duabus pinnis basalibus lateralibus prominentibus* 16 (12–23) cm. longis atque pinna centrali paulo longiore plerumque constans, *pinnis in segmenta ultima impariter lunata bis divisis*; *segmenta 17* (12–21) mm. lata latere anteriore 8 (6–10) mm. longo, latere basali 14 (8–22) mm. longo, *segmenti pedicellis* 2.6 (1.5–4.0) mm. longis, *soris tribus ad decem omnibus in segmentis*, 4 (1–10) mm. longis, *sporis abortivis*.

A terrestrial fern of moderate size; stem a branching rhizome, 6 (4–8) mm. thick, of indefinite growth but dying off basally; roots up to at least 5 cm. long, borne around the leaf bases, and bearing numerous branches at irregular intervals, the whole root system covered with pale-yellow hairs 1 mm. long; stem apex and sides protected by shiny, dark reddish-brown, elongate-triangular paleae, 1–2 mm. long, 0.5–1.0 mm. broad at base and narrowing to a filiform apex; leaves 2–3 times divided, long-petiolate, 44 (25–60) cm. in total length, the petioles 21 (13–29) cm. long and 1.0–1.5 mm. thick, the blades deltoid, 23 (20–30) cm. long and 25 (15–35) cm. wide; petioles lustrous purplish or maroon-black and naked except for a few paleae remaining at the base; blade subhorizontally oriented when alive, with 3–7 large lateral pinnae, but the two basal ones usually much larger, 16 (12–23) cm. long, than those above, the frond

thus appearing to comprise usually 3 major pinnae, the two laterals roughly one-half to two-thirds as long as the whole blade and the one central pinna; basal lateral pinnae provided with one or two long basiscopic segments each; rachis lustrous maroon-black, conspicuously angular at the origins of the two large basal pinnae, but becoming nearly straight distal to them; tertiary segments unequally lunate, averaging 17 (12–21) mm. across at the widest point, the inner (or anterior) of the two sides 8 (6–10) mm. long and the lower (or basal) side 14 (8–22) mm. long; stalks of the segments hair-like but rigid, 0.1 mm. thick, 2.6 (1.5–4.0) mm. long, lustrous black; lamina dull-green, glabrous; venation subflabellate, free, the veins forking 2–5 times; sterile margins of the lamina finely toothed with occasional broad sinuses 1–2 mm. in depth at intervals of 2–10 mm.; sori marginal, 3–10 per segment, with whitish, thick, false indusium averaging 4 (1–10) mm. in length and 1 mm. in breadth; sporangia containing spores of irregular size and shape.

Type specimen. "*Adiantum*. Probably hybrid *jordanii* × *pedatum*. Original single plant found near Pepperwood, Sept. 1895, from which this is propagated in garden at Eureka. Sept. 16, 1924." Joseph P. Tracy 6868b (Herb. Univ. Calif. no. 249775).

Specimens examined. CALIFORNIA. From near Pepperwood, Humboldt County, cultivated at Eureka, Tracy 6868a, 6868b (UC), cultivated at Berkeley, Nicolls (UM); from near Garberville, Humboldt County, cultivated at Garberville, Neeman (US, no. 1916165); from south fork of Gualala River, Sonoma County, cultivated at Inverness, Logan (US, no. 2084573); from near Guerneville, Sonoma County, cultivated at Inverness, Logan (US, no. 2081080); from Bear Valley, Marin County, cultivated at Petaluma, Syme (US, nos. 982424, 982425, 983776, 983777).

This fern may be distinguished from *Adiantum pedatum* by the overall shape of its frond: in mature blades of *A. pedatum* there are normally 5–9 major divisions of the blade and the blade is broadly fan-shaped; in × *A. tracyi* there are usually only three major divisions, the two lateral pinnae and the somewhat longer central pinna, and the blade is more nearly triangular. Also the sori of the hybrid average two to three times as long as those of *A. pedatum*. From *A. jordanii* the hybrid is most readily separated by the form of the blade also: in *A. jordanii* the leaf is broadly lanceolate and pinnate in construction and the pinnae are gradually reduced in size from base to apex; in × *A. tracyi* the blade is relatively much broader at the base and it usually shows a rather sudden reduction in pinna length from the basal pinnae to those above. The pinnae of *A. jordanii* are almost perfectly flabellate while those of the intermediate have a strongly developed lower margin about twice as long as the inner margin.

The fern described here appears actually to be intermediate between the two presumed parental species in practically every respect. To show this, the writer took the fifteen best-developed leaves available of the

hybrid plant and an equal number of mature specimens of each parent and measured them for some obvious characteristics to give a picture of the quantitative conditions. The results of these measurements, in terms of averages and ranges for each character, are shown in Table 1. Whole

TABLE 1. COMPARISON OF *× ADIANTUM TRACYI* WITH ITS HYPOTHETICAL PARENTS

	<i>A. jordanii</i>	<i>× A. tracyi</i>	<i>A. pedatum</i>
Length of Blade (cm.)	19 (11-25)	23 (20-30)	22 (15-35)
Length of Petiole (cm.)	14 (6-20)	21 (13-29)	29 (15-40)
Blade/Stipe Length (%)	136	109	76
Length of lower side of segments (mm.)	9.3 (5-15)	13.6 (8-22)	20.0 (13-25)
Length of inner side of segments (mm.)	7.1 (4-11)	7.5 (6-10)	7.6 (6-10)
Lower side/inner side length of segments (%)	131	181	263
Length of segment stalks (mm.)	4.1 (1.5-8.0)	2.6 (1.5-4.0)	0.7 (0.0-1.5)
Length of proximal sorus (mm.)	4.8 (2.0-10.0)	4.2 (1.5-9.0)	1.7 (0.5-4.0)
Distance between segment attachments (mm.)	15.8 (11-21)	12.4 (10-16)	8.9 (5-12)

leaves were measured for blade length, petiole length, and blade-petiole ratios. The differences in segment shapes of the three taxa could be expressed clearly in respect to lengths of inner margins and basal margins and the ratios of these two lengths. As shown in Table I, the inner (or anterior) and lower (or basal) margins in *A. jordanii* are nearly equal in length while in *A. pedatum* the lower margin is almost three times the length of the inner margin. The stalks of the segments in *A. jordanii* are much longer than those of *A. pedatum*. The greater remoteness of the segments in *A. jordanii* as compared to the other parent and the hybrid was determined by measuring the distance between segment stalks along the top side of the middle of the largest basal pinna. For uniformity the sori of the three taxa were measured on two central segments of the largest basal pinna, and for each segment the proximal sorus alone was used. In all these characteristics measured and averaged, the hybrid turned out to be intermediate, except for blade length which is, however, approximately the same in well-developed leaves of all three entities.

With the exception of the terminal segments of each pinna, the segments (ultimate pinnules) of *A. jordanii* and of *A. pedatum*, as pointed out above, are conspicuously different in their outlines (fig. 2, cf. a and c). Copeland (1947, p. 78) in describing the genus *Adiantum* writes as follows: "lamina typically broad, and pinnately decompound with dimidiate or flabellate pinnules." The present hybrid fern thus combines the two characteristic pinnule forms of the genus, the "dimidiate" (i.e., appearing as if one half of the pinnule is lacking, with a strong vein running along the basal margin) of *A. pedatum*, and the "flabellate" (i.e., fan-shaped,

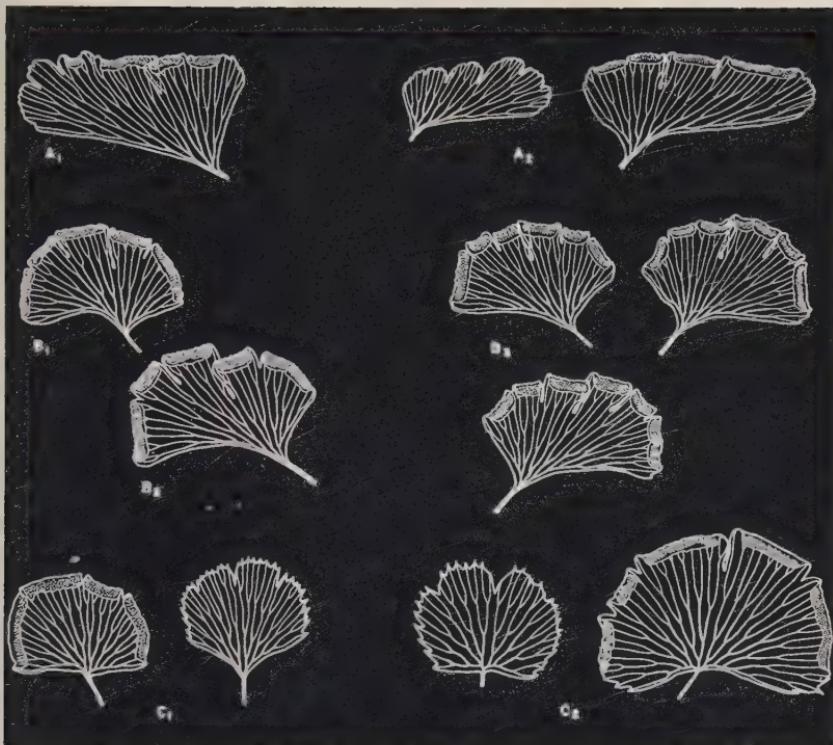


FIG. 2. Comparison of segment structure. A. *Adiantum pedatum*: A₁, Cheboygan County, Michigan, Ehlers 1560; A₂, Delta County, Michigan, Grassl 7232 (both UM). B. \times *Adiantum tracyi* (*A. jordanii* \times *A. pedatum*): B₁, near Garberville, Humboldt County, California, Neeman; B₂, Syme Garden, US no. 982424; B₃, Logan Garden, US no. 2081080 (all US). C. *Adiantum jordanii*: C₁, La Jolla, California, Clements 1914; San Benito County, California, Wiggins & Ferris 9353 (both UM).

without a clear costulate development at any point) of *A. jordanii*. In the dimidiate segment of *A. pedatum* there is vaguely evident a costule (the "midrib" of the segment) which runs along the proximal side of the pinnae and from which the secondary veins originate, all of the secondary veins directed toward the distal side. But in the flabellate type of *A. jordanii*, no costule or main vein can be detected at all, and the segment thus appears to be entirely midribless—that is, the segment is entirely dichotomous in vascular structure. The question of which of these pinna types represents the more basic condition in the genus *Adiantum* is one which seems not to have been dealt with before, and it would be inappropriate here to discuss the problem in any detail. However, it should be noted that there are indeed species of *Adiantum* which do possess centrally costate segments, i.e., segments with a more or less central axis giving rise to veins equally on both sides (e.g., *A. dolosum* with free veins and *A. olivaceum* with reticulate veins). And there are numerous species in which

a progressive shift in costule position from the central position to the proximal side of a dimidiate pinna can be illustrated (e.g., the series of *A. latifolium*, *A. villosum*, *A. caudatum*, *A. curvatum*, and *A. klotzschianum*). It seems perfectly possible that the flabellate condition of *A. jordanii* could have been derived independently of the dimidiate type of *A. pedatum* in evolution from a basic and primitive pinnule-type in the genus in which the costule was centrally located. On the other hand, the dimidiate type could equally well have given rise to the flabellate type by way of an intermediate stage such as that exemplified in the pinnule form of $\times A. tracyi$. There are other normal species in the genus in which the pinnules are similar to those of $\times A. tracyi$ and may be looked upon either as lop-sided flabellate segments or as shortened and broadened dimidiate segments.

The most interesting morphological aspect of $\times Adiantum tracyi$ is its leaf architecture. This combines the pinnately-constructed leaf of *A. jordanii* (an over-all leaf type which characterizes practically all of the some 200 species of the genus) with the uniquely organized leaf of *A. pedatum*. The latter species, which in California is commonly called the "five-finger fern" in reference to the division of its leaves, possesses blades distinguished by "stalks forked at the top, the outwardly curving forks each bearing 3 to 8 pinnae . . ." (Jepson, 1923). As was first pointed out by Slosson in 1906, the seemingly dichotomous leaf form of *A. pedatum* (an extremely rare over-all leaf form known only in this species, in the Old World *A. hispidulum*, and in the Mexican *A. patens*) is in reality a much-modified pinnately constructed leaf. I have designated this (1952) the "displaced-midrib type of dichotomous leaf," because of the peculiar orientation of the morphological rachis. While superficially most of the leaf blades seem to have regularly dichotomous major axes, they are actually asymmetrically constructed, the true midrib being present but modified in relative development and orientation as compared with fern leaves typically in which the rachis is simply a more or less straight, *central* axis of the frond. In the juvenile leaves of *A. pedatum*, as shown by a heteroblastic series of progressively larger leaves produced on a maturing rhizome, the early ones are pinnate in form like the mature leaves of *A. jordanii* and they have a typical strong central axis (fig. 3, c). But in progressively larger leaves of *A. pedatum* one of the basal lateral pinnae becomes enlarged and re-oriented, and the rest of the blade, including the midrib, is correspondingly changed so that the enlarged basal pinna finally equals the rest of the blade; it becomes practically a mirror image except for the extra pinnule on the pinna shank of the dichotomy. Tracings of the axes of blade bases of *A. pedatum* (fig. 3, a), $\times A. tracyi$ (fig. 3, b), and *A. jordanii* (fig. 3, c) made from dried herbarium specimens show that the intermediate fern possesses blade construction which closely matches an intermediate stage in the heteroblastic series of leaves of *A. pedatum* (cf. Wagner, 1952, fig. 3, the two middle rows of leaves). The study of this hybrid, then, emphasizes the differences between leaves of



FIG. 3. Tracings of the major axes of the blade bases in pressed herbarium specimens. A. *Adiantum pedatum*: A₁, Branch County, Michigan, McVaugh 11298; A₂, Charlevoix County, Michigan, Reis 652A; A₃, Houghton County, Michigan, Richards 927; A₄, Alpena County, Michigan, Grassl 7230 (all in UM Herb.). B. \times *Adiantum tracyi* (*Adiantum jordanii* \times *A. pedatum*): B₁-B₄, George Syme Garden (original plants said to have come from Bear Valley, Marin County, California) Syme (specimens in US Herb.); B₅-B₇, C. C. Hall Garden, Nicolls (UM); B₈, George Syme Garden, Eastwood (US). C. *Adiantum jordanii*: C₁, Oakland Hills, Lemmon; C₂, Cupertino, California, M. E. Jones; C₄, Cupertino, California, Fisher; C₅, near San Francisco, California, Harrington (all UM).

different heteroblastic stages. In *A. pedatum*, presumably, specific genes, different from and (or) in addition to, those of the genus as a whole, must be present which control the formation of a unique leaf type only in the mature state. In the juvenile state these controlling factors show no effect, and the basic leaf construction is then like that of *A. jordanii*. In the hybrid fern, the successively larger leaves of juvenile plants must pass through a series like that of *A. pedatum* but the heteroblastic series leading to the peculiar form of the latter can apparently proceed no further than approximately half-way because of the influence from *A. jordanii*.

The degree of variation of leaf form seen in $\times A. tracyi$ considerably exceeds that of the parents. Mrs. Hall some years ago called to my attention that no two fronds are alike on one plant; she had discussed a plan at that time to save a large series to show the complete range of variation but it apparently never materialized. A single plant of $\times A. tracyi$ may show in the variation in architecture from leaf to leaf the same sort of irregularity that seems to characterize other hybrid ferns in which the parents differ widely in specific foliar features, as was found recently in the case of *Polystichum acrostichoides* $\times P. lonchitis$ from the Bruce Peninsula (Wagner and Hagenah, 1954), in which certain microscopic details of venation proved to be irregular, and in several examples of hybrids among the species of Appalachian *Asplenium* in which the lobulation of the leaves is irregular (Wagner, 1954).

SUMMARY

A plant intermediate between *Adiantum jordanii* and *A. pedatum* has been found growing wild in three counties of California. It has proved vigorous and hardy in horticulture and reproduces readily by rhizomes. The plant is described here as a hybrid taxon, $\times Adiantum tracyi$ C. C. Hall, because of its intermediacy in a number of obvious characters, its sporadic distribution in nature and its association there with the parents, and the abortion of its spores. The leaf segments combine the "dimidiate" type of *A. pedatum* with the "flabellate" type of *A. jordanii*. The over-all architecture of the leaf blade is of morphological interest in combining the "displaced-midrib" type found in *A. pedatum* with the more ordinary pinnately-constructed blade type of *A. jordanii*, but the branching of the rachis is variable.

Department of Botany,
University of Michigan, Ann Arbor.

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DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See MADROÑO 9:257-258. 1948.)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
LILIACEAE <i>Furcraea</i> * <i>Roezlii</i> André	n = 30	H. Arnott & M. S. Cave, UC ¹	<i>Arnott</i> 54, UC ¹	Univ. Calif. Campus, Berkeley, California
<i>Nolina</i> * <i>Beldingii</i> Brandegee	n = 19	M. S. Cave, UC	<i>Carter & Ferris</i> 3331, UC	San Francisco, Baja Calif., Mexico
ROSACEAE <i>Purshia</i> * <i>tridentata</i> DC.	2n = 18	M. S. Cave, UC	(From seed) <i>B. Pearson</i>	Janesville, Lassen County, California
EUPHORBIACEAE <i>Argythamnia</i> * <i>Brandegei</i> var. <i>intonsa</i> (Jtn.) Ingram	n = 13	F. Chisaki & J. Ingram, UC	<i>Ingram</i> 227, UC	Gila Mountains, Yuma County, Arizona
SOLANACEAE <i>Acnistus</i> <i>arborescens</i> (L.) Schlecht.	n = 12	C. B. Heiser, Jr., IND ¹	<i>Heiser</i> 3578, IND	Turrialba, Prov. Cartago, Costa Rica
<i>Capsicum</i> <i>macrophyllum</i> (HBK.) Standl.	n = 12	"	<i>Heiser</i> 3483, IND	La Lola, Prov. Limón, Costa Rica
<i>maculatum</i> Standl. & Morton	n = 12	"	<i>Heiser</i> 3534 IND	La Paz, Prov. Heredia, Costa Rica
<i>stenophyllum</i> Morton & Standl.	n = 12	"	<i>Heiser</i> 3535 IND	"
<i>stramoniiifolium</i> (HBK.) Standl.	n = 12	"	<i>Heiser</i> 3575 IND	San José, Prov. San José, Costa Rica

(continued on p. 206)

*Prepared slide available.

¹ Symbols for institutions are those listed by Lanjouw and Stafleu, Index Herbariorum, Part I. Second edition, 1954, Utrecht.

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
<i>Capsicum tetramerum</i> Standl. & Morton	n = 12	C. B. Heiser, Jr., IND	Heiser 3470 IND	La Carpintera, Prov. Cartago, Costa Rica
<i>Lycianthes multiflora</i> Bitter	n = 12	"	Heiser 3514 IND	Turrialba, Prov. Cartago, Costa Rica
<i>Solanum Cervantesii</i> Lag.	n = 12	"	Heiser 3491 IND	Robert, Prov. Cartago, Costa Rica
<i>ciliatum</i> Lam.	n = 12	"	Heiser 3516 IND	Turrialba, Prov. Cartago, Costa Rica
<i>jamaicense</i> Mill.	n = 12	"	Heiser 3518 IND	"
<i>parcebarbatum</i> Bitter	n = 12	"	Heiser 3510 IND	"
<i>salviifolium</i> Lam.	n = 12	"	Heiser 3509 IND	"
<i>torvum</i> Swartz	n = 12	"	Heiser 3511 IND	"
<i>umbellatum</i> Mill.	n = 12	"	Heiser 3632 IND	"
LOBELIACEAE				
<i>Clermontia *oblongifolia</i> Gaud.	2n = 22	S. Carlquist, UC	Carlquist H 4 UC	Mt. Olympus, Oahu, T. H.
<i>Cyanea *angustifolia</i> Hillebrand	n = 12	"	Carlquist H 5 UC	"
<i>Laurentia *carnosula</i> (H. & A.) Gray	n = 11	"	Mason 14439 UC	Sierra Valley, Sierra County, Calif.
COMPOSITAE				
<i>Baileya *multiradiata</i> Harv. & Gray	n = 16	"	Carlquist 323 UC	San Marino, Los Angeles County, Calif.
<i>Brickellia *peninsularis</i> Brandegee var. <i>amphithalassa</i> Robinson	n = 9	"	Carlquist 382 UC	Socorro Island, Mexico
<i>Perityle *socorroensis</i> Rose	n = 19	"	Carlquist 368 UC	"
<i>Tetramolopium *humile</i> Hillebrand	n = 7	"	Carlquist H 18 UC	Haleakala, Maui, T. H.

NOTES AND NEWS

TERMS USED TO DESIGNATE TYPE MATERIAL. Although the principal terms used to designate type material are sufficiently defined in the International Code of Botanical Nomenclature as adopted in 1950 (Regnum Vegetable v. 3, 1952, pp. 17-18), there is still laxness among botanists in the application of these terms. For those who do not have access to that volume, the definitions there given may be repeated here with some legitimate modifications in wording, and a few collateral ones added.

A *holotype* (generally called "type") is the single specimen on which the description of a new taxon is based; the term is also somewhat loosely applied to the basic unit of preparation (sheet or packet of macroscopic specimens, slide of microscopic) on which a taxon is based. In the strict sense such units, if consisting of more than one specimen, are composed of syntypes.

A *syntype* (originally *cotype*, a term still used by some authors) is each of two or more specimens on which a taxon is based by an author who does not designate a holotype.

A *lectotype* is a single type selected by a subsequent author from among syntypes. By definition it has to be part of the original material.

A *paratype* is each specimen other than the holotype (or syntypes) cited in the original description by an author who designated a holotype (or syntypes).

An *isotype* is a duplicate of the holotype (duplicate in the sense that it is a part of the collection [e.g., Pringle 8248] on which a taxon was based). Even the most careful collectors occasionally distribute more than one entity under a given number, and an isotype should always be carefully compared with the original description before basing conclusions on it.

A *neotype* is a substitute type selected by a later author in a case where he has convincing proof that no holotype, syntype, paratype, or isotype is in existence. Any material can be selected as a neotype, but it is best to select a topotype, if practicable.

A *topotype* is a specimen (other than the type itself) from the type locality. It is not actually a type in any proper sense, but, especially in zoology, it may have the study value of a duplicate type.

The terms *isosyntype*, *isolectotype*, *isoparatype*, and *isoneotype* are available to designate duplicative material of the specimens that served for syntype, lectotype, paratype, and neotype respectively.

The most nearly complete glossary of terms relating to type material is given by D. L. Frizzell in American Midland Naturalist 14:637-668. 1933, and there is a discussion of some of the commoner terms of most use in botany by the writer in Rhodora 45:481-485. 1943.

With the above definitions in mind it can be seen that in the two papers on Cucurbitaceae by K. M. Stocking published in numbers 3 and 4 of this volume of Madroño, the term lectotype is used in the following places to designate specimens that are actually neotypes: on p. 96 (*Echinopepon minimus*), p. 126 (*Marah watsonii*), p. 130 (*M. fabaceus* var. *agrestis*), p. 132 (*M. macrocarpus*). On p. 86 the so-called lectotype of *Echinocystis lobata* should have been designated instead as a neotype but has no validity as such since Michaux's type is still in existence. The so-called "types" of *Echinopepon confusus* (p. 90), *E. nelsonii* (p. 92), *Marah major* (p. 134), and apparently also *Echinocystis scabrida* (p. 130) are lectotypes.—S. F. BLAKE, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, Maryland.

Some publications of interest follow:

Drawings of British Plants, by Stella Ross-Craig. Part VII. Leguminosae. 76 pls. 1954. 12s. net. Part VIII. Rosaceae(1). 40 pls. 1955. 8s. 2d. net. G. Bell and Sons, Ltd., London.

Plant Genera, Their Nature and Definition, a symposium by G. H. M. Lawrence, I. W. Bailey, A. J. Eames, R. C. Rollins, M. S. Cave, and H. L. Mason, with an introductory essay on *Generic Synopses and Modern Taxonomy* by Theodor Just. *Chronica Botanica*, Vol. 14, No. 3, 1954. \$2.00. The *Chronica Botanica* Co., Waltham, Mass., and J. W. Stacey, Inc., San Francisco

The Ferns and Fern Allies of Minnesota, by Rolla M. Tyron, Jr. i-xx, 1-166, 207 figs, 85 maps, 2 pls. 1954. \$4.00. University of Minnesota Press, Minneapolis.

The Ferns and Fern Allies of New Mexico, by H. J. Dittmer, E. F. Castetter, and O. M. Clark. University of New Mexico Publications in Biology No. 6:1-139, 55 figs. 1954. This and the preceding will prove useful to both layman and botanist.

CALIFORNIA BOTANICAL SOCIETY
PUBLISHERS OF MADROÑO

REPORT OF THE TREASURER FOR 1955

RECEIPTS:

Balance on hand in commercial account, January 6, 1955.....	\$ 720.50
From memberships and subscriptions	1,817.00
From sales of back numbers of <i>Madroño</i>	634.50
Receipts from annual dinner	129.50
Received as authors' share of publication costs.....	349.15

Total receipts \$3,650.65

DISBURSEMENTS:

Credited to endowment fund from sales of back numbers.....	\$ 634.50
Treasurer's expenses	75.98
Corresponding Secretary's expenses	76.62
Editorial Secretary's expenses	10.00
Cost of annual dinner	124.80
Cost of printing, binding, and mailing <i>Madroño</i> , Volume 13, Numbers 1, 2, 3, and 4.....	2,264.60

Total disbursements \$3,186.50

BALANCE ON HAND IN COMMERCIAL ACCOUNT, American Trust Co.,
Palo Alto

\$ 464.15

ENDOWMENT FUND:

Palo Alto Mutual Savings and Loan Association, balance on hand January 5, 1956	\$3,066.52
Accrued interest	97.70
Realized from two United States War Savings Bonds, Series F, matured January 1, 1955.....	200.00
From sales of back numbers of <i>Madroño</i>	634.50

American Trust Company, savings account, balance Janu-
ary 5, 1956

\$3,998.72

..... \$ 365.25
Accrued interest

7.33

372.58

Total endowment \$4,371.30

Accounts audited and found correct:

W.M. HIESEY, Auditor
January 23, 1956

RICHARD W. HOLM,
Treasurer for 1955